

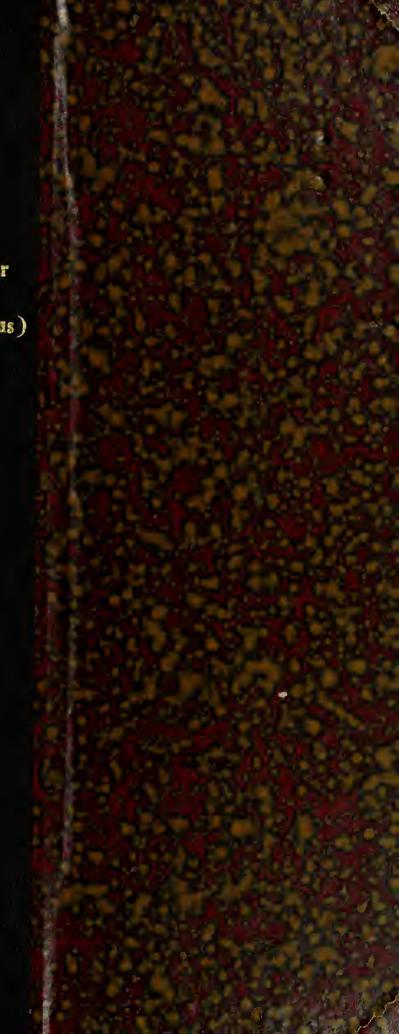
GOURLEY

The Development of the Inner Ear of the Lizard. (Sceloporus Undulatus)

Zoology

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THE DEVELOPMENT OF THE INNER EAR OF THE LIZARD, (SCELOPORUS UNDULATUS)

BY

MARY JANE GOURLEY A. B. University of Illinois, 1909.

THESIS

Submitted in Partial Fulfillment of the Requirements for the

Degree of

MASTER OF ARTS

IN ZOOLOGY

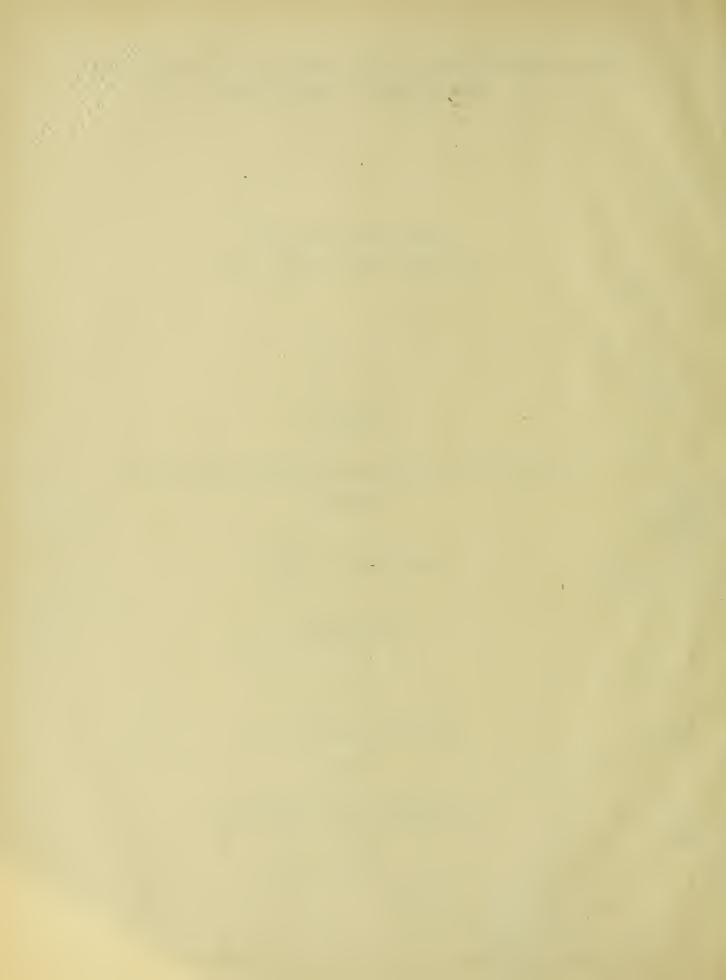
IN

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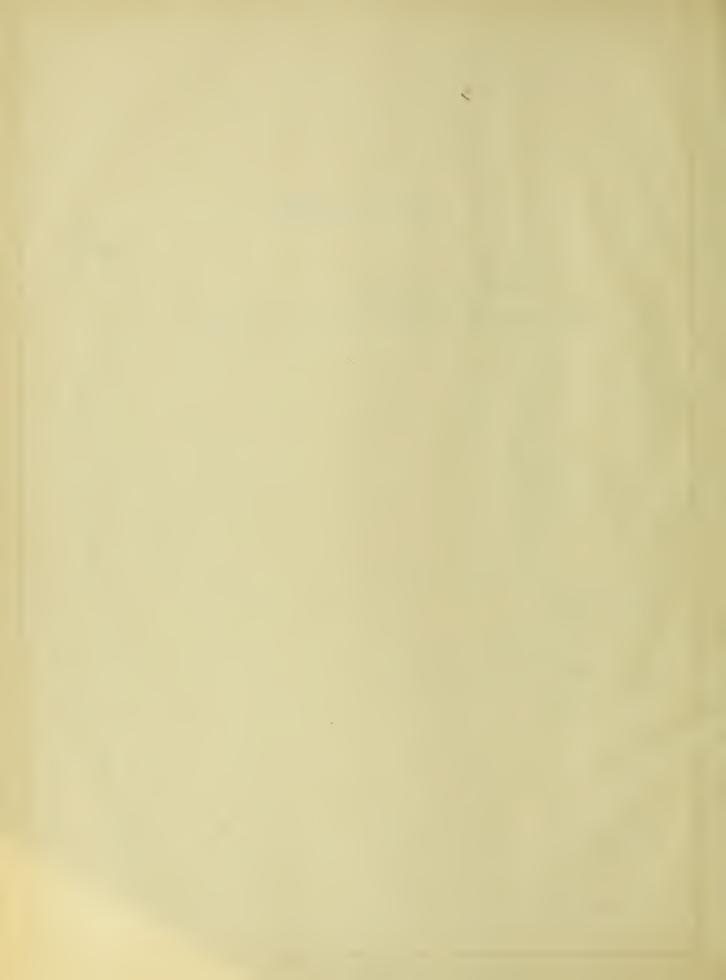
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Final Examination



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T INTRODUCTION

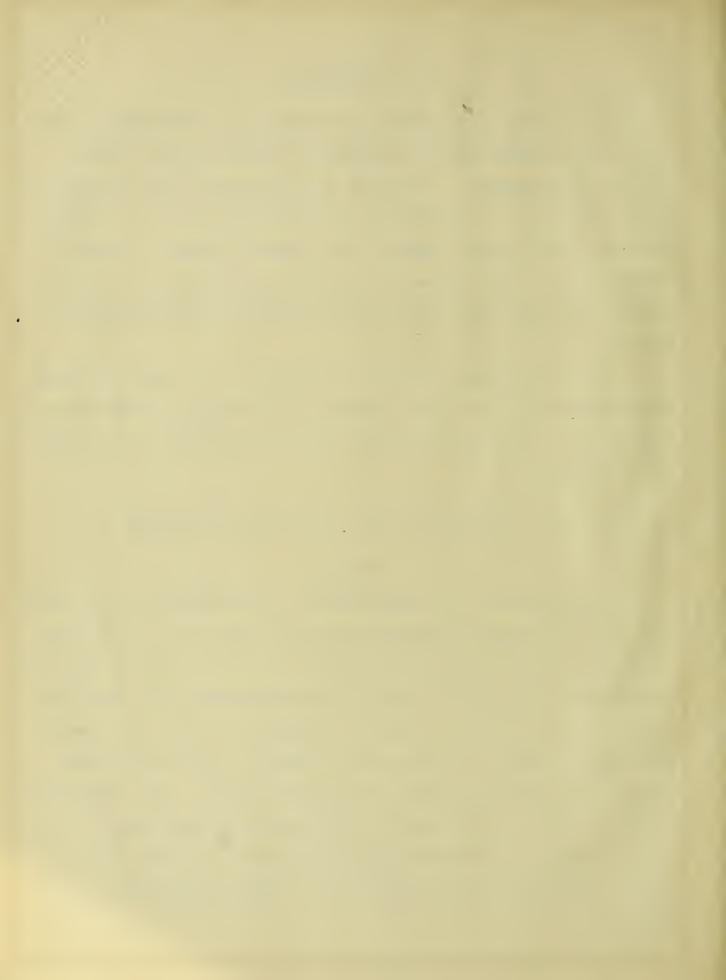
The following paper describes the embryonic development of the inner ear and especially the membranous labyrinth of the lizard (Sceloporus undulatus). Saggital and transverse serial sections of various stages in the development of these animals were studied and wax reconstructions were made of the important stages. Then the sensory area of each section was outlined and painted on the model, so that they showed the limits of the sensory and non-sensory epithelium.

I wish to express my thanks to Professor J. S. Kingsley, under whose direction the work was pursued, for his helpful criticisms and suggestions. I am also indebted to him for the use of several series of slides.

II DEVELOPMENT OF THE INNER EAR OF THE LIZARD

Stage I

The first phase of the development of the inner ears is a thick-ened patch of columnar ectodermal cells on either side of the head immediately behind the anlage of the VII - VIII nerve as in all other vertebrates. This patch of specialized ectodermal cells soon sinks (figs. 1 and 2) forming a slightly elongated oval pit, which gradually becomes deeper, and, as shown in Stage I, its walls are more abrupt on the posterior than on the anterior side. This difference between the walls is the result of the process of infolding of the sensory anlage which progresses more rapidly in the lower and especially the posterior margin of the pit than at other parts of the wall.



Between this and the next stage (Stage II) unfortunately no material was available showing the successive steps of the closure of the pit into the otic vesicle.

Stage II

In Stage II the process of invagination has been completed. otic capsule has been entirely closed, and the connection of the otic ectoderm with the exterior is entirely lost. Even the endolymph duct has lost its connection with the outer world. In the otic capsule at this stage two parts may be recognized, dorsally a saccus endolymphaticus and ventrally a vestibular pcuch, the two connected by a short endolymph duct. Both the saccus and vestibular pouch are compressed from side to side, the vestibular pouch being over twice the size of the saccus in every dimension. Viewed from the side the saccus endolymphaticus is somewhat rhomboidal in outline, and extends anteriorly beyond the level of the anterior end of the vestibular pouch, while the endolymph duct, connecting its vento-posterior angle, extends down on the inner face of the vestibular sac to open into it at about the upper fourth of its height. Viewed from the lateral or medial side the vestibular pouch has an oval outline. From the point of entrance of the endolymph duct into the vestibular pouch a marked ridge extends posteriorly and ventrally on the outer surface of the medial side of the vestibular pouch, the external expression of the atrium. The lagena is already outlined as a small diverticulum from the postero-ventral margin of the vestibular pouch, and extends anteriorly and medially. There is a well marked groove on the medial surface between the atrial and lagenar projections which extends upwards behind the atrium and marks off the anlage of the ampulla of the posterior canal from the rest of the pouch. On the



posterior part of the external surface of the vestibular pouch is a horizontal ridge, the first expression of the lateral canal, but at this stage there is little except position to differentiate the superior canal from the rest of the pouch. Judging from the model at this stage the lateral canal is the first to develop.

In this stage all of the ventral and posterior walls and the ventral portion of the medial, lateral, and anterior surfaces of the vestibular pouch are composed of a continuous area of thickened sensory epithelium. The non-sensory areas include the anlagen of the superior and posterior canals (with the exception of the ampullar anlagen) and the ductus and saccus endolymphaticus.

On the internal surface of the vestibular pouch at this stage there is an oblique ridge extending inwards and downwards from the lateral wall (fig. 3), the beginning of the separation of the lateral from the posterior canal; the ventral limit of the former being marked by a slighter ridge (fig. 3) while a third ridge on the medial wall of the pouch indicates the dorsal limit of the atrium (fig. 3) and continues forward and slightly upwards to separate the ductus endolymphaticus from the anterior portion of the anlage of the posterior canal. Near the lower part of the pouch a fourth fold runs parallel to the ventral surface, becoming more prominent posteriorly, and then turns upwards, marking the ventral extent of the atrium (fig. 3), distinctly separating it from the lagena.

Stage III

In a slightly older embryo (Stage III) the vestibular pouch is still compressed but the saccus endolymphaticus has swollen into an approximately globular form. The atrial ridge which was prominent



externally in the previous stage, has flattened out, the medial surface being now approximately flat. On the external surface the lateral canal is more prominent than before, rising abruptly from the vestibular pouch on its dorsal and anterior side, but passing gradually into the ventro-posterior portion of the vesicle and the lagena. The superior canal is next in extent of differentiation, its posterior boundary being evident on the external surface, but there is no corresponding groove between it and the rest of the vestibular pouch on the medial surface. The lagena has become more prominent and relatively larger than before, its apex being directed medially and ventrally, but it is not sharply marked off at its base from the atrial region.

As in Stage II, the sensory area is still unbroken and shows but slight changes. It is very evident, however, that the lateral canal is wholly included within it.

The dorsal and ventral ridges of the lateral canal are more prominent (fig. 4) than they were in the last stage. The medial and lateral walls have met and fused (fig. 5) for a short distance at the posterior region of the vestibular pouch, partially separating the lagena from the posterior ampulla. A slight outpushing of the medial wall marks the position of the atrium.

Stage IV

Although the endolymph sac is considerably larger in Stage IV it is still globular in outline and the endolymph duct has hardly increased in length. No marked features can be seen on the medial surface of the vestibular sac, which is still compressed, though the development of the canals gives the whole a wider appearance. The lagena is now marked off from the atrial region by a slight constriction.



tion and is directed ventrally and posteriorly, the former medial inclination being lost. The anlage of the lateral canal now forms a broad shelf directed laterally and somewhat dorsally. The superior canal is no further developed than it was in the previous stage, but the posterior canal is more prominent and extends as a marked projection on the lateral surface of the vestibular pouch. The order of the formation of canals differs from this in Amblystoma (Norris) as the lateral canal is the first to develop, followed in order by the superior and posterior canals. Krause, on the other hand, found in all groups of vertebrates studied by him (including Sauropsida) that the superior canal is the first to develop, next the posterior, and lastly the lateral.

At this stage the sensory area does not cover relatively as large a portion of the lateral and medial walls as before, the difference being largely due to a greater increase of the dorsal portion of the pouch. The junction of the dorsal side of the shelf of the external canal with the lateral vestibular wall marks the dorsal extent of the sensory epithelium of the lateral wall (fig. 6) and the sensory area on the medial side reaches to about the same level.

On the inner surface the dorsal of the two ridges limiting the lateral canal has extended ventrally and is approaching the ventral ridge (fig. 6) but the two have not met. The ampulla of the posterior canal is, as before, separated from the lagena by the coalesced walls of the vestibular pouch, and the partition formed by them is continuous with the ridge below the posterior canal, although the latter has not united with that from the medial wall (fig. 6).

Stage V

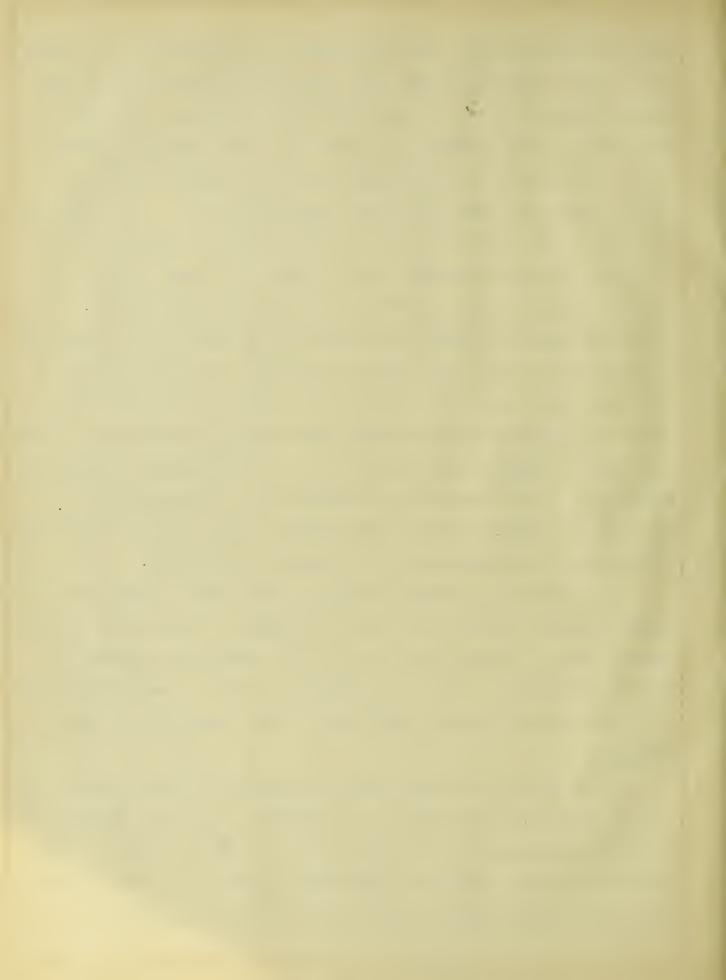
This stage shows a marked advance over Stage IV. The condition



of the sections did not allow any certain determination of the shape of the saccus endolymphaticus, but they clearly showed that it now extends medially so that it lies dorsal to the brain. lymph duct is more elongated than before. The vestibular pouch shows the beginning of a differentiation into saccule and utricle. and the ampullar regions have been separated from it. The lagena is slightly larger than before, and, as the portion connecting it with the pouch has become somewhat constricted, this region is more distinctly differentiated from the vestibular pouch than earlier. ridges mentioned in Stage IV as indicating the limits of the anlagen of the several canals have now met and fused so that the lumina of the canals have been differentiated from that of the rest of the utricular region of the vestibular pouch except at either end. These processes and that of the absorption of the fused areas, progressing essentially in the way so often described for all vertebrates, results in the formation of the three canals which are as distinct but not as long or as arcuate at this stage as in the adult.

The distinctively canular portion of the lateral canal is no longer sensory, but like the other two canals is included in the non-sensory area. The ampullae of all of the canals are composed of sensory epithelium. All of the saccule and utricle below the level of the opening of the endolymph duct is still lined with sensory epithelium.

On the inner surface the posterior ampulla communicates with the base of the vestibular pouch at its posterior end, while the superior and lateral ampullae open into its anterior ventral portion. The posterior end of the lateral canal opens directly into the main portion of the pouch, but the superior and posterior canals unite to



to form a common tube, the crus commune, by means of which they communicate with the main vesicular cavity.

Stage VI

The utricle in Stage VI is beginning to show a distinct separation from the saccule. A transverse constriction separates the utricle into an anterior or cephalic part and a posterior or caudal part. The anterior region constitutes the general utricular cavity from which a diverticulum, the recessus utriculi. extends ventromedially from the region of the ampullae of the superior canal. The posterior part of the utricle consists of a central sinus utriculi commune, into which the crus commune opens from above, while laterally it connects with the sinus utriculi lateralis of the lateral canal and below with the sinus utriculi inferioris of the posterior canal. The saccular region is approximately hemispherical and the lagena. which now extends ventrally and medially from it, has become greatly elongated, its distal end being more attenuated. The canals are relatively smaller in diameter but are longer and more arcuate in outline. All of the ampullae are well differentiated from the remaining portions of the canals. The superior and lateral ampullae are joined to the main utricle while the posterior ampulla is united to the sinus utriculi inferioris.

In the ampullae the sensory epithelium has become restricted to the ventral and a little of the external walls of the superior and lateral ampullae. In the posterior ampulla it still covers all except the dorsal wall. These sensory areas are still continuous with the area which includes the external and ventral walls of the main utricle, the lower portion of the saccule, the sinus utriculi commun-



is, and the lagena. In Amblystoma, at this stage of development, the sensory area has been divided into sensory patches, since the division takes place shortly after the differentiation of the canals.

Some changes have taken place on the inner surface. The posterior ampulla now communicates with the sinus utriculi inferioris and the superior and lateral ampullae with the main utricular cavity.

All divisions of the utricle are in open communication. The opening between the utricle and saccule is very wide. The lagena opens into the ventro-posterior region of the saccule and the ductus endolymphaticus into the dorsal part of the median wall of the saccule.

Stage VII

In Stage VII, although all parts of the membranous labyrinth have increased in size, there are no marked changes. Development has taken place most rapidly in a cephalo-caudad direction, which has resulted in carrying the two ampullae of the superior and lateral canals farther forward. The saccus endolymphaticus shows an increase in size relatively greater than that of other parts of the labyrinth.

The inner surface and sensory areas show very little change from conditions in the previous stage. The opening between the utricle and saccule, the beginning of the utriculo-saccular canal, has become a little smaller.

Stage VIII

This last stage studied shows an enlargement of all parts. The utricle is more distinctly separated from the saccule than it was in the previous stage. The saccus endolymphaticus shows an enormous growth in a median direction, and the sacs of the two sides have fused



dorsal to the brain but they do not as yet communicate as they do in the Amphibia. Each saccus is flattened in the transverse plane, and when viewed from in front or behind is still somewhat rhomboidal in outline. The constriction between the saccule and lagena has become greater so that they are only connected by a small canal.

Although the sensory epithelium is still a continuous area, it shows the beginning of the divisions which eventually result in the definitive maculae and cristae of the adult. The area common to the superior and lateral ampullae and the utricle is almost completely separated from the area of the sinus utriculi communis. Only a small band connects the sensory epithelium of the lagena with the saccule and the posterior ampulla with the sinus utriculi inferioris.

Very few changes have taken place on the inner surface. The utriculo-saccular canal is considerably narrower although it is still very large. The ductus reuniens leading from the saccule into the lagena is a short and narrow canal.

III SUMMARY

The auditory pit soon becomes a closed vesicle which consists of a vestibular pouch and an endolymphatic appendage. The semicircular canals are formed from a portion of the pouch by the meeting and fusion of the walls of the vesicle and the absorption of the intervening vestibular walls. The part of the pouch which is not involved in the formation of the canals gives rise to the utricle, saccule, and lagena.

The sensory area at an early stage includes all of the closed vesicle except the anlagen of the superior and lateral canals--not including the ampullae. The sensory epithelium decreases in area proportionally as development advances until it is finally limited to



the ventral portion of the ampullae, utricle, and saccule, but it continues to include all of the lagena.

Changes take place on the inner surface simultaneously with the changes on the exterior. Ridges arise from the walls of the pouch and coalesce, forming the canals which communicate with the utricle at both ends. Constrictions separate the utricle from the saccule, leaving them connected by the utriculo-saccular canal. A small canal, the ductus reuniens, opens from the lagena into the saccule and another opening exists between the saccule and ductus endolymphaticus.

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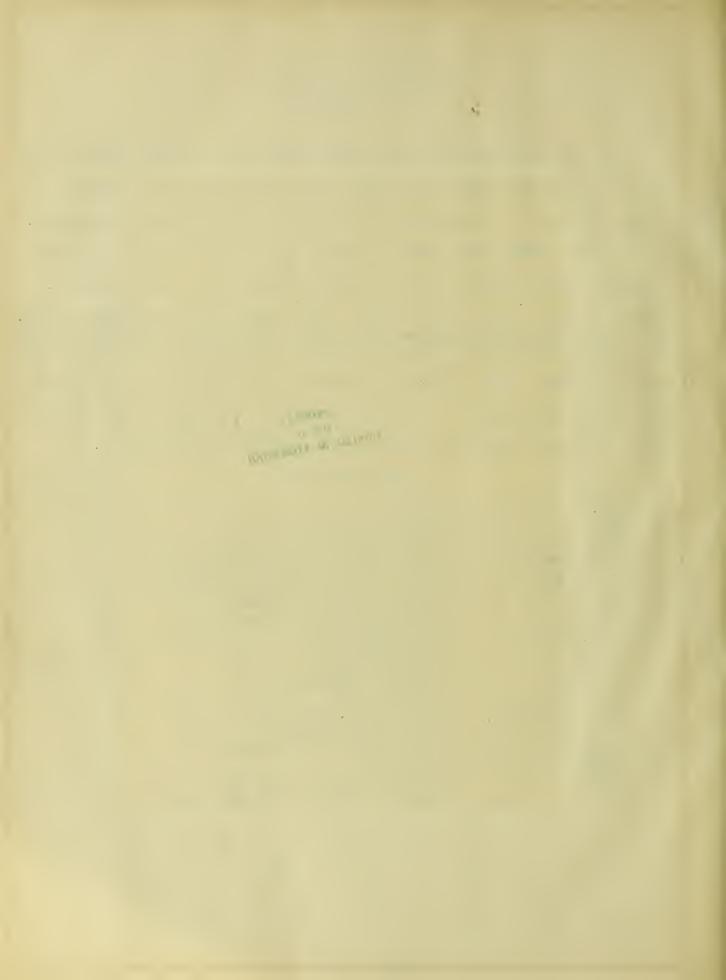
EXPLANATION OF PLATES

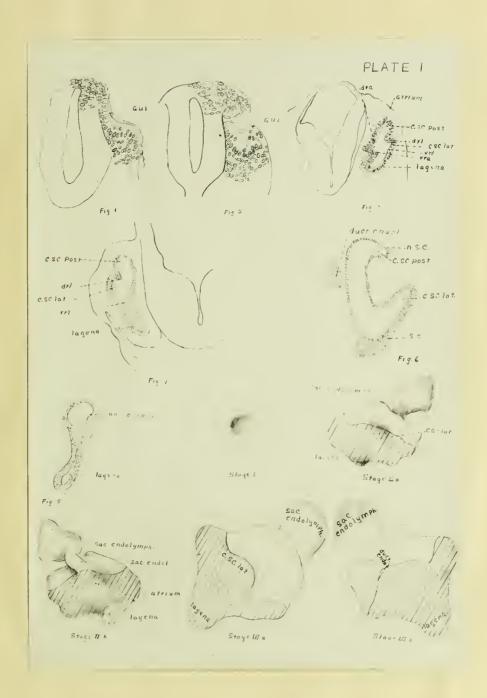
I, II, AND III

Most of the figures (drawn approximately to the same scale) represent wax models, made from serial sections of the most important stages studied, of the membranous labyrinth of Sceloporus undulatus. To these are added a few sections especially of the earlier stages. The cross lined portions on the models indicate the sensory areas. Figures I, IIb, IIIb, IVb, Vb, Vlb, VIIb, and VIIIb are medial views, and figs. IIa, IIIa, IVa, Va, VIa, VIIa and VIIIa are lateral views. The figures indicated by Arabic numerals are camera drawings of cross sections (figs. 1-6). Fig.1 is a section of a stage which is earlier than any of the models. Fig.2 is a section of Stage I, Fig. 3 of Stage II, Figs. 4 and 5 of Stage III, and Fig. 6 of Stage IV.

Abbreviations

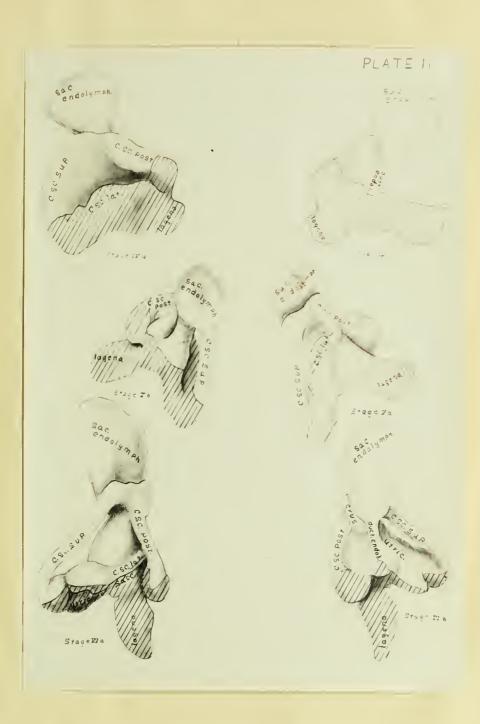
amp. - - - - ampulla: aui - auditory involution crus - - crus commune c. sc. lat. - - ductus semicircularis lateralis c. sc. post. - - ductus semicircularis posterior c. sc. sup. - - ductus semicircularis superior dra. - - dorsal ridge of atrium drl. - - dorsal ridge of lateral canal duct. endol. - - ductus endolymphaticus lagena - - - ductus lagena n. s. e. - - non-sensory epithelium rec. utr. - - - recessus utriculi sacc. - - - - sacculus sac. endolymph. - saccus endolymphaticus s. e. - - - sensory epithelium sinus utric. inf. sinus utriculi inferoris utric. - -_ _ utriculus vra. - -- - ventral ridge of atrium vrl. - - - - ventral ridge of lateral canal





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